

THE PHYLOGENY OF THE GALL MITES AND A NEW CLASSIFICATION OF THE SUBORDER PROSTIGMATA OF THE ORDER ACARINA.

By H. E. EWING,

Bureau of Entomology, U. S. Department of Agriculture.

Of all the major groups of the Acarnia it is doubtful if any are more aberrant than the gall mites, and but few show such unity of organization or sameness of habits. Because of this there has been in the past but little evidence upon which to establish any natural affinities between them and any of the other groups, while suggestions as to their origin have been but little more than conjectures.

RECENT VIEWS IN REGARD TO THE AFFINITIES OF THE GALL MITES.

By way of both introduction and review, here are given some of the more recent views in regard to the relationships of the gall mites.

In 1910 Dahl committed himself to the belief that the gall mites were related to the other Acarina through the Tarsonemidæ. He regarded the genus *Tarsonemus* as representing a transitional stage between the Eriophyidæ and the Acarina proper. This belief was held largely because of the nature of the last pair of legs. These legs, normally developed in the free-living Tarsonemidæ, are shortened and almost rudimentary in some of the parasitic species. He found in this group the tendency toward leg reduction which has been so completely effected in the Eriophyidæ.

Banks (1915) champions the Tarsonemid theory. In his well known treatise on the mites he states: "The Eriophyidæ are, perhaps, more closely related to the Tarsonemidæ than to any other group. Many of the Tarsonemidæ feed exposed on the leaves or stems of a plant; some of them cause swellings or deformities of the plant, and some have the body more or less distinctly segmented. Moreover, in several genera of the Tarsonemidæ there is a tendency toward reduction in the number of legs, and in other genera the hind legs are very

slender and of little use in walking." Banks' basis for a belief in Tarsonemid relationship is the existence of similar feeding habits of the two groups and the fact that in the Tarsonemidæ there is "a tendency to the reduction in number of the legs."

Oudemans (1910) states in his review of the families of the Acarina* that the Eriophyidæ are probably most nearly related to the spinning mites or "perhaps even an earlier stage of the Tetranychide." This suggestion that the gall mites are an earlier stage of the Tetranychidæ requires some evidence for its support and an elaboration of explanations based on such evidences. Until such are brought forward the suggestion falls far short of a theory which can be used constructively in the advancement of our knowledge of natural relationships.

A THEORY AS TO THE PHYLOGENY OF THE ERIOPHYIDÆ.

It is my purpose here to state and then substantiate a definite theory as to the origin of the gall mites. The theory is this: The gall mites, a highly aberrant and degeneratively specialized group of phytophagous parasites, have arisen through the process of profound morphological change and adjustment, from a recently discovered group of gall-making spider mites. This group the writer has recognized as a family, the Phytoptipalpidæ, and it is to be regarded as a transitional group between the Eriophyidæ and the Tetranychidæ. I would not derive the gall mites from any living species of the family Phytoptipalpidæ or even from the genus *Phytoptipalpus*; yet it appears from the evidence at hand that the two or more living species of *Phytoptipalpus* are barely out of a line of direct descent between the spider mites and the gall mites.

THE GENUS PHYLOPTIPALPUS—ITS DISCOVERY AND THE INTERPRETATION OF ITS RELATIONSHIPS.

The genus *Phytoptipalpus* was established in 1905 by Tragardh for a very peculiar mite species named by him *paradoxus*, which was found in galls of an African species of *Acacia*. The species was very peculiar in several respects. It evidently was a true gall making species, yet did not belong to the group known as the gall mites. The mites were red,

*Oudemans, A. C. A Short Survey of the More Important Families of Acari. Bul. Ent. Research, Vol. 1, pp. 105-119, figs. 1-22.

with a somewhat elongate body, and had even in the adult stage only six legs. The mouth-parts were all but identical with those of the Eriophyidæ, while the tarsal armature was quite similar in some respects to that of certain genera of the Tetranychidæ. The species was oviparous and differed very markedly in its development from that of the spider mites.

Recently the present writer has described* another species of *Phytoptipalpus* taken from the jujube tree (*Zizyphus jujuba*) in India. This species is quite similar to the one described by Tragardh. It makes galls on the bark of the jujube and lives inside of these galls. So similar is this species to Tragardh's *paradoxus* that any phylogenetic significance that attaches to the one should usually apply to the other. The two species are not only congeners, but are very closely related.

The interpretation which the present writer places on the meaning of the peculiar structure of *Phytoptipalpus* is exactly the reverse of that given by Tragardh. Tragardh held that the similarity between the mouth-parts of *Phytoptipalpus* and the Eriophyidæ was due to convergence, hence attached no phylogenetic significance to them and was content to place his new genus in the subfamily Tetranychinæ next to the genus *Tenuipalpus*. He states: "Die so geartete umbildung der Mundteile von *Phytoptipalpus*, welche bei der Gattung *Tenuipalpus* gewissermassen vorbereitet ist, ist ein sehr schönes Beispiel von Konvergenz unter dem Einfluss von gleichen ausseren Lebensbedingungen. Die Gattung *Phytoptipalpus* lebt nämlich wie die Phytoptiden in Pflanzengallen und ernährt sich von den Pflanzensaften."

This resemblance which Tragardh explains as being due to convergence, the present writer would ascribe as due chiefly to inheritance. In other words, the Eriophyid type of mouth-parts is similar to the *Phytoptipalpus* type, not because both Eriophyids and the *Phytoptipalpi* inhabit galls, but chiefly because they have the same ancestry. This thesis I now will attempt to both explain and establish. It involves a consideration of other characters than the mouth-parts and other mites than the two groups mentioned. We will start, however, with the mouth-parts. I will compare first the mouth-parts of the Eriophyidæ with the species of *Phytoptipalpus* with which I have worked. The name of this species is *Phytoptipalpus transitans*.

*Proc. Ent. Soc. Wash., Vol. XXIV, p. 103.

THE MOUTH-PARTS OF THE ERIOPHYIDÆ AND THOSE OF
PHYTOPTIPALPUS TRANSITANS EWING.

The close resemblance between the mouth-parts of *Phytoptipalpus* and those of gall mites were clearly recognized when Tragardh established the genus for his species, *paradoxus*. This resemblance was emphasized by giving the genus its name, *Phytoptipalpus*.

In the Eriophyidæ the mouth-parts have been reduced and consolidated. The palpi are no longer free, but have become shortened and fused with their bases to become a trough (Fig. 1) in which lie the needle-like chelicerae. Evidences of segmentation is retained by the palpi, and three indistinct segments are usually recognized. The chelicerae (Fig. 1, c) are minute, very slender and needle-like. Those of *Eriophyes pyri* I have detached from the body and find that they arise

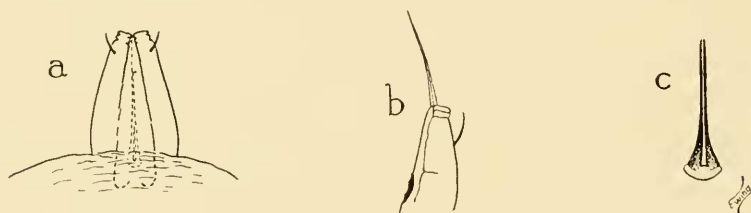


Fig. 1. Mouth-parts of *Eriophyes pyri*; all drawings greatly and equally enlarged. A, dorsal view of capitulum; b, side view, showing the palpus, the extended chelicerae and the ventral mouth-opening; c, dorsal view of chelicerae.

from a common base (Fig. 1, c). The oral opening is conspicuous and is situated on the ventral floor of the fused mouth-parts. This position is typical for other Acarina.

In *Phytoptipalpus* the palpi are reduced and fused so as to form a trough for the chelicerae. This fusion has been even more complete than in the Eriophyidæ, as only a single segment remains discernible. The chelicerae are small, very slender and needle-like. They are elbowed near their bases, and the latter are lodged in a well defined mandibular plate. On the ventral side of the fused maxillæ is a conspicuous opening. According to Tragardh it is through this opening in *paradoxus* that the chelicerae are thrust. In *transitans* the chelicerae lie in an almost capillary gutter and are thrust from the tip of the capitulum and not at all through this opening. According

to the view of the present writer this opening is no other than the mouth-opening which leads to the pharynx.

So nearly alike are the mouth-parts of *Phytoptipalpus* and those of the Eriophyidæ, that to explain their complete homology it is only necessary to point out their few differences. The maxillæ and the maxillary palpi are practically the same in both cases except in *Phytoptipalpus* only a single fused palpal segment is distinguishable, while in the Eriophyidæ three are usually recognizable. The stylets of the chelicæræ of the two groups are the same, except that in *Phytoptipalpus* they are elbowed near the base. In *Phytoptipalpus* and all of the spider mites the bases of the chelicæræ are lodged in a flat chitinous structure which may be in certain species

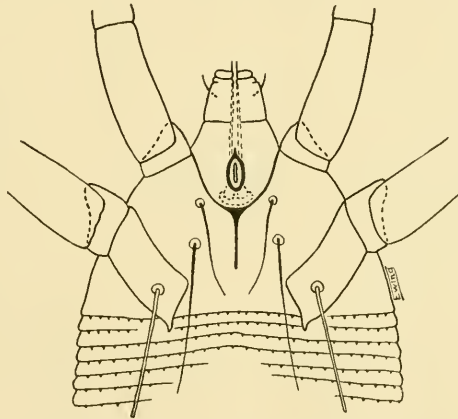


Fig. 2. Ventral view of anterior part of body of *Eriophyes pyri*; greatly enlarged.

protrusible. This structure has long been known as the mandibular plate. In working on the homologies of the mouth-parts of the Eriophyidæ the writer has found that in *E. pyri* that the chelicæræ both arise from a common base, and that this base could logically be regarded as the same structure which in the Tetranychidæ and in *Phytoptipalpus* is called the mandibular plate. It is a greatly reduced structure in the Eriophyidæ and in fact is vestigial.

The pharynx and oral opening in the two groups of mites are, as I have found, identical, although Tragardh regarded the ventral opening in *paradoxus* as being a provision for the thrusting out of the chelicæræ.

THE TARSAL ARMATURE IN THE ERIOPHYIDÆ AND IN
PHYTOPTIPALPUS.

The Tarsonemid theory of the origin of the Eriophyidæ fails utterly to explain the presence of the peculiar tarsal armature of the gall mites. In the Eriophyidæ each tarsus is armed at its tip with a simple claw and below it with the pectinate structure known as the "feather hair" (Fig. 3, *c*). The so-called "feather hair" is composed of an almost straight central part from which branch off below four or five pairs of barbs.

Of all the groups of the Acarina no other group gives as close an approximation to the Eriophyid type of tarsal armature as the red spiders, or spider mites. Of the various genera of

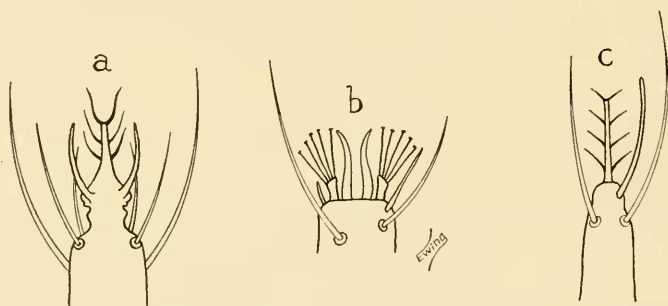


Fig. 3. Tarsal armatures of *Syncaligus*, *a*; of *Phytoptipalpus*, *b*; and of *Eriophyes*, *c*.

the spider mites the genus *Syncaligus*, a genus showing many relationships with *Phytoptipalpus*, has a tarsal armature most nearly like that of the Eriophyidæ. In this genus there is a ventral structure, the empodium (Fig. 3, *a*), which differs from the "feather hair" of the Eriophyidæ only in being stouter and having one or two less barbs, or branches. In addition to the empodium in *Syncaligus*, two tarsal claws are present. It is from the *Syncaligus* type of tarsus that the tarsal armature of both *Phytoptipalpus* and the Eriophyidæ have probably been developed; in *Phytoptipalpus* by the splitting of the empodium into two and an increasing of the number of its branches, and in the Eriophyidæ by the atrophy of one of the tarsal claws. That one of the tarsal claws is easily lost is shown repeatedly in the Acarina. Even in the Tetranychidæ it is now

taking place in the genus *Paratetranychus*, has taken place in genera *Tetranychus* and *Oligonychus*; while in another genus in the same family, the genus *Anychnus*, both claws are gone.

Thus it is seen that not only is the Eriophyid tarsus structurally more nearly related to a type found in the Tetranychidæ, but it can be homologized with the latter type, and the evolutionary changes necessary to give the exact Eriophyid tarsus are actually observed now in progress in the group from which we would derive the Eriophyids.

THE FORM OF THE BODY IN THE ERIOPHYIDÆ AND THE TETRANYCHIDÆ.

Next in morphological importance to the structure of the mouth-parts and of the tarsal armature and number of legs in the Eriophyidæ, is probably the form of the body. It is in nearly all species vermiform, in fact one of the common names of the suborder of gall mites is Vermiformia. In addition, the long-drawn-out body is ringed with many circular folds of the integument.

This ringed, vermiform condition is only matched in the hair follicle mites of all the other major mite groups, and the hair follicle mites are so different from the gall mites in practically all other respects that a suggestion of their affinity with the Eriophyidæ has never even been made.

Undoubtedly the vermiform body of a hair follicle mite is an adaptation—an absolutely necessary adaptation—to its life in the hair follicles, and with almost complete assurance we can accept it that their origin and descent is from some ectoparasitic zoophagous group, probably from the parasitic Cheyletidæ as held by Hirst.

Searching elsewhere in the different groups of the Acarina, instances of a vermiform tendency are found in several of them and as has been noted, exists in the Tarsonemidæ, more particularly, however, in the female, for the males of the Tarsonemids are as a rule short-bodied. In the Tetranychidæ we find not only examples of this tendency to develop the vermiform type of body, but it is correlated with the development of the gall-producing habit.

In such free-living and active genera as *Tetranychus* and *Paratetranychus* the body is stout, but in other genera where the attacks of the mites are so restricted that they live almost

as fixed parasites, the body becomes more flattened and usually elongate. Then in such species as *Stigmaeus floridanus* Banks, which lives in colonies at the bases of imbricated leaves of the pineapple, the body becomes markedly lengthened. Finally, in the genus *Phytoptipalpus* we find not only a lengthened body, but in the male particularly the body ringed in almost the same way as in the Eriophyidae. (Fig. 4).

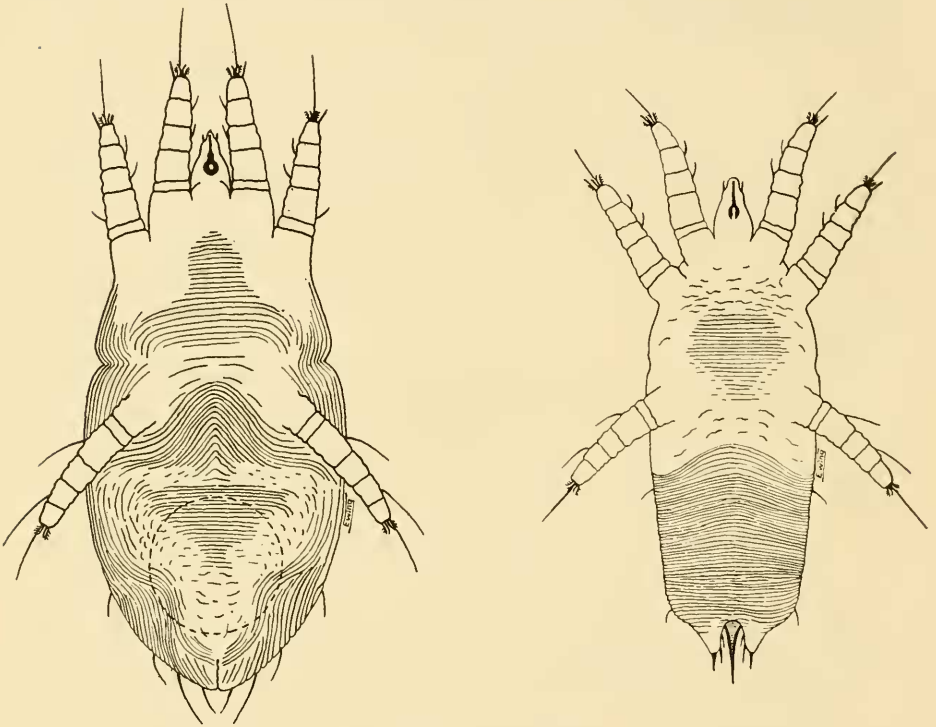


Fig. 4. *Phytoptipalpus transitans* Ewing. Ventral views of male (smaller individual) and female (larger individual) equally enlarged.

SUMMARY OF RELATIONSHIPS.

Thus it is found that in what probably constitutes the three most important groups of morphological structures in the gall mites, that these structures can be homologized with those of the same groups in the *Phytoptipalpidæ*. Further, it is observed that all modifications necessary to give the types of these three important group of characters in the *Eriophyidae* can be explained, and what is more important, the processes of change

can actually be traced out not only in other groups of mites, but in the Tetranychidae and the Phytoptipalpidae the two families held to be the most nearly related to the Eriophyidae. Lastly the morphological changes thus traced out are correlated with changes in habits which give finally a high degree of approximation between the hypothetical ancestral group and the group whose origin is to be explained.

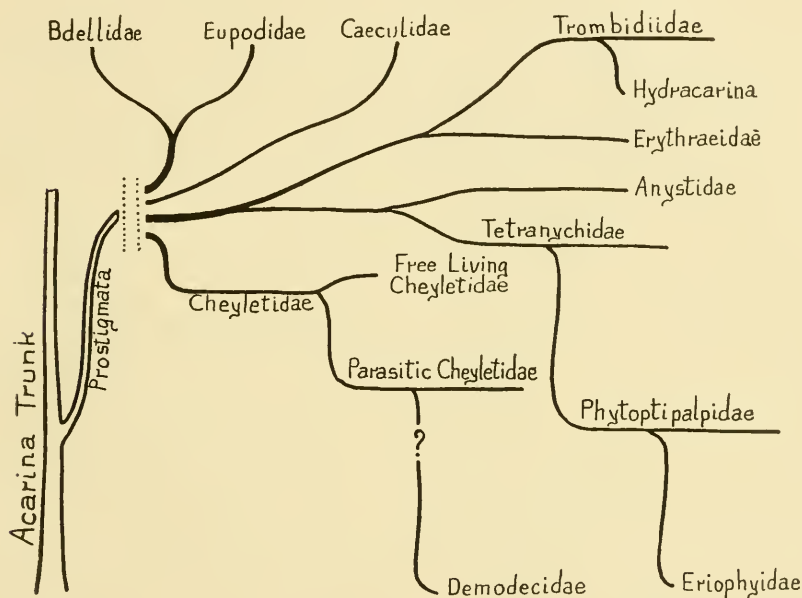


Fig. 5. A "tree" diagram illustrating the origin and relationships of the families of Prostigmata.

The relationship and origin of the Eriophyidae is indicated in the following diagram (Fig. 5). For sake of completeness the relationships of other families of the order Prostigmata are also shown according to the writer's interpretation.

The same relationships can be shown in the form of a key to the families of Prostigmata; not so clearly, yet some practical advantage may be obtained in the key by enabling one to place properly a given species to family. A key to the families of the suborder Prostigmata is here given in the form of a new classification. In this classification the mouth-parts are made, to a large extent, the basis for family differentiation.

A NEW CLASSIFICATION OF THE SUBORDER PROSTIGMATA.

- A. Chelicerae chelate; adapted for biting; palpi without thumb.
 - Section ADACTYLOGNATHA
 - B. Mouth-parts not formed into a beak; palpi neither geniculate or raptorial.....*Eupodidae*
 - BB. Mouth-parts formed into a conspicuous beak; palpi either geniculate or raptorial.....*Bdellidae*
 - AA. Chelicerae either falcate or needle-pointed, adapted for piercing.
 - B. Legs usually adapted for swimming. Aquatic mites,
 - Section HYDRACARINA
 - C. Mouth-parts not situated on a beak. Fresh water mites,
 - Hydrachnidae*
 - CC. Mouth-parts situated on a more or less distinct beak. Marine mites.....*Halacaridae*
 - BB. Legs not adapted for swimming. Mites not aquatic.
 - C. Legs composed of more than three segments; palpi provided with a thumb, except in degenerate forms, in which case they are fused with the maxillae.....Section DACTYLOGNATHA
 - D. Chelicerae falcate; palpi free, five-segmented and with the last segment always formed into a thumb.
 - E. First and second legs provided with processes bearing large spines; integument with large chitinous shields,
 - Caeculidae*
 - EE. First and second legs without processes bearing spines; integument without any large chitinous shield.
 - F. Cephalothorax with a rod-like structure at the bottom of a median dorsal groove; legs stouter and usually with swollen tarsi.....*Trombidiidae*
 - FF. Cephalothorax without rod-like structure and median dorsal groove; legs more slender and tarsi never swollen.....*Anystidae*
 - DD. Chelicerae not falcate but either styletiform or needle-like; palpi frequently reduced in size and number of segments, and variously modified.
 - E. Cephalothorax with a rod-like structure at the bottom of a median dorsal groove; tarsi not attenuated, but on the contrary frequently swollen; body well clothed with short setae.....*Erythraeidae*
 - EE. Cephalothorax without rod-like structure and median dorsal groove; tarsi tapering from base to apex; body sparsely clothed with setae of varying lengths.
 - F. Each tarsus provided with either a pectinate distal appendage or tenent hairs, or both of these; palpi moderate or small; phytophagous in habits.
 - G. Adults with four pairs of legs; palpi free; never producing galls.....*Tetranychidae*
 - GG. Adults with less than four pair of legs; palpi greatly reduced and united ventrally to form a trough for the needle-like chelicerae; usually producing and inhabiting galls.
 - H. Body not vermiform; adults with six legs; each tarsus provided with two claws and two "feather hairs;" gall makers.
 - Phytoptipalpidae*
 - HH. Body vermiform; adults with only four legs; each tarsus provided distally only with a single claw and "feather hair". *Eriophyidae*
 - FF. Tarsus usually without pectinate appendages and always without tenent hairs; palpi usually large; predaceous or parasitic in habits.....*Cheyletidae*
 - CC. Legs stumpy and composed of only three segments; body vermiform.
 - Parasitic mites.....Section BRACHYPODA
 - One family.....*Demodecidae*